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A Contribution to the Life History of the Euchromid Moth, *Aethria carnicauda* Butler[1]

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(Plates I & II)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B. W. I.," William Beebe, (ZOOLOGICA, 1952, Vol. 37, No. 13, pp. 157-184).]

ON February 27, 1953, at Simla, Arima Valley, Trinidad, a caterpillar, No. 5330, was collected. It measured 28 mm in length and changed during the next 24 hours into a chrysalid. Examination revealed that the bare, dead twig on which the caterpillar had pupated was encircled by nine complete and separate whorls of hairs, five beneath and four above the cocoon. We had no idea of how these whorls were made, but their use seemed to be as a chevaux-de-frise to discourage marauding ants or other enemies from access to the chrysalid area of the twig. On March 12 a euchromid moth emerged, *Aethria carnicauda* Butler.

The earliest reference I can find to any similar larval achievement is a small illustration dated April, 1871, together with a short note dated December 1882, by Fritz Müller (Kosmos, VI Jahrg., 1883, Band XII, p. 449). In this case the euchromid moth was *Dinia aeagrus* (Cramer) (= *Eunomia eagrus*), a species widely distributed through Mexico and Argentina, but not recorded from Trinidad. There is no account of the method of formation of the whorls.

The details of the whorls in Müller's illustration differ in a number of respects from those made at Simla by *Aethria carnicauda*. Müller's whorls are much closer together, barely separately distinguishable. The two ends of the chrysalid are protected by the slanting hairs of the adjacent whorls. That nearest to the caudal end is imperfect, a full half of the total number of radial hairs being linearly distributed along the twig, throughout the length of the pupa. There is no hint of the hammocklike cocoon, composed of the shorter body hairs in our specimens. Nor is there any indication of the disposition of the brushlike tufts of black hairs. The recurved character of the hair tips is not apparent.

These data prepared us for the development and for the defense mechanism of another larva of the same species. The following is an account of the ontogeny and the making of the whorls of larva number two.

This caterpillar was collected by Kenedy on a leaf blade of the Black-and-White Trinidad Sedge, *Scleria melaleuca* Schl. & Cham., at Simla, on February 10, 1953. No. 5322.

Its chronology is as follows: Collected February 10, length 9 mm. The dates of five molts were February 12, 16, 21, 27 and March 4. The night of March 9 and 10, whorls formed, larval adult length 27.5 mm. March 11, pupated. March 21, moth emerged.

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When collected, the caterpillar was small (9 mm) and long-haired. It was divided into thirds by its color pattern: head and tail black, mid-zone grayish-green, almost invisible against the leaf tissue. The hairs were very long at head and tail. Superficially the larva looked like two small, adventitious spots, separated by a short extent of green grassblade.

The method of eating was by gnawing longitudinal slits through the blade, utilizing the tissue between the two thick ribs. The night-time position was lengthwise, beneath the leaf.

It molted on February 12, the mid-section still being green, with black extremities. From the first thoracic segment arose a pair of stout, red tubercles. Between these was a mid-dorsal, vertical, brushlike tuft of black hairs. This character was repeated at the hinder end of the body. The head was large and pale amber. The general effect was one of our tussock moths.

The body was covered with tufts of slender, fine, whitish hairs, with recurved tips. The dorsal body rows were short and stellate. The lateral were longer, while those from the three thoracic segments, and the corresponding posterior ones, were very long. The anterior elongate hairs were inclined forward and extended far beyond the head, while the posterior ones were directed backward.

At this stage the larva fed by lying longitudinally along one of the two main ribs, and, swinging the head from side to side, chewing a section from the outer edge to the mid-rib, and then shifting back for another slice. The larva slowly backed down the leaf, but otherwise made no shift.

The edges and surface of the sedge were densely covered with very hard, sharp spines, which bothered the larva not at all. Every now and then it raised the tail and voided a pellet to some distance, all without cessation of feeding. Another proof of excellent digestive powers was the eating of the cast skin, spines and all.

On March 4 the larva molted for the fifth time. When it first emerged from the old skin, it appeared as a sodden mass, the body hairs flattened and stuck together, overlaid longitudinally by a solid slick of what would be the long, black head tuft. The corresponding caudal tuft extended out, back and up as a matted wisp. Soon the hairs began to separate and now ensued irregular flexings of the whole larva. The tail bent far up and forward, and the head reared back until the two extremities met and rubbed against each other. The caudal wisp was drawn across the head, back and forth, each time freeing a few more hairs. In half an hour all the hairs were dry, free and in place.

The body, in this instar, was slaty black with two longitudinal, pale lemon yellow lines, one latero-dorsal, the other lateral. Head pale buff. Third anterior segment with two, swollen, red and yellow tubercles on the single segment, joined transversely across the back by a narrow area. From each of the tubercles arose anteriorly-directed tufts of very long, slender hairs. From the fourth segment sprang the median, black, brushlike tuft.

Behind the tubercled segment were two segments bearing tufts of exceedingly long hairs. Counting these two, there were seven segments giving rise to a lateral row of short pale tufts, between the white lateral lines, with other rows of tufts on the upper and lower light lines themselves. The succeeding two segments carried swollen, reddish tubercles, with long, posteriorly-directed hairs, corresponding to the similar anterior character. The larva now ate obliquely across the entire leaf, tough veins, spines and all. It fed during the day, and rested at night.

The caterpillar, seen in profile against the light, showed distinctly only the head and body, and the fore-and-aft black, upright brushes of hairs. The multitude of long pale hairs appeared only as a faint, silvery-gray mist, with the pale brown curved tips slightly more distinct. Under forty-power magnification the long hairs of the caterpillar were seen to be not simple, but covered everywhere with a dense growth of spinules or minute, stiff hairlets. These were directed at an acute angle up the length of the hair. They must be of material help in consolidating the structural strength of the overlapping bases of the whorls. The multitude of sharp spinules also offer ample points of attachment and entanglement for the viscid drops and the strands of spirals of spun silk.

On March 9 the larva was eating ravenously. It chewed obliquely across the stem, slowly backing down until it reached the botton. Then it shifted to an adjoining sedge blade, climbing up to the top and working back. It averaged four pellets every half hour. The fresh pellet was pale green, a broad oval in shape, with flattened ends. It was composed of compressed bits of grass tissue, some of which contained as many as 30 to 40 plant cells.

In the afternoon of March 9 the larva devoured one and a half long grass blades, stopping when 125 mm above the base. Here it took up a position lengthwise beneath the stem and remained quiescent for the rest of the afternoon and evening.

At 8 P.M. there was no change. At 9 o'clock we found two completed whorls of hairs *below* the larva, and the little creature was at work. It was inverted on the blade, weaving with its head and neck, back and forth, a spiderlike

cross-webbing of silk between the radiating hairs. It frequently broke the strand of web and began anew.

When it was through, it turned around and climbed up the stem until its posterior end was about 10 mm above the uppermost whorl. We soon discovered that any bright or white light interfered with the activities of the caterpillar, so fastened a red filter to a flashlight, to which the larva paid no attention. (This was an Eastman "wratten" Filter A, No. 25, cutting off practically all light except the orange and red, i.e., everything shorter than 590 mμ. To the extraordinary complexity of its routine the larva added the apparent handicap of working in the dark.

The larva now climbed 40 mm up beyond the lower whorls and began violent contortions with head and thoracic segments, all of which were exceedingly mobile. It rubbed its head sideways, back and forth against the grass blade, bending down the long hairs which studded the surface. The result was to rub or massage the base of the hairs. It would push and push and suddenly there came a snap or jerk, as the hairs freed themselves from the pressure. Then it would curl around laterally into a tight circle, hanging on only with the 2nd and 3rd pairs of prolegs. For a considerable time this twisting and rubbing continued, while now and then a hair was taken between the mandibles and "mouthed" before being dropped again.

Forty mm above the uppermost lower whorl a new one was begun. The mouth parts were rubbed back and forth on one place on the grass, and with a hand lens I could see the spinneret in full operation. The silk strand was strung with viscid drops and a foundation of sticky silk was deposited. Suddenly the larva reached back and the mass of thoracic hairs was bent far forward. It seized a hair, gave a strenuous pull and plucked it out, holding it upright in the mandibles. Then it rubbed the base into the sticky mass and bound it there. Watching the removal of the next few hairs I detected a regular method. The hair was seized, the mandibles slid down to the base, then up again a short distance, then a moment's hesitation, and a powerful jerk disengaged the root. Thus a short extent of basal hair projected beyond the mandibles. When the hair was pushed against the foundation and glued there, the extra extent of hair projected slightly. No hair was attached by the extreme end. They slightly overlapped and furnished support for the rest making up the whorl. Thus as the whorl increased, each radial hair was partly braced by the short, projecting end of the others. The measuring routine was a normal part of the performance.

The first few hairs were wide apart, sometimes with a 90° divergence, then the intervening spaces were filled in. After the planting of each hair, it was tilted up and down, so that in some way, by some invisible guide, it was finally oriented on to the same horizontal level with its fellows. In addition, the curved tips of the hairs invariably pointed downward in the proximal whorls, and upward in the distal series.

After the planting of each hair, elaborate binding with web took place, and the construction of two to six guy cables, above, on the upper side. These extended from the whorl to the grass blade, in length once or twice the hair's extent. Thus the downpull of gravity was guarded against. There was a decided difference in the amount of viscid drops on the silk at different times. It was present in copious quantities in building the foundation and in affixing the hairs, but was almost absent in the laying of the connecting webs between spokes and in the guy strands. The uppermost whorl was completed in fifteen minutes, with three 2-minute rests.

In comparison with the observed finished whorls of larva number 5330, the attachments of the present whorls were arranged around a small round twig, which formed a perfect hub for the wheel. In the present instance, the base was a wide-spread M, in cross section of the grass blade. So only about three-fourths of a circle was possible, the remaining gap being closed by the extension, cross-wise, of the extra hairs, lying close to the wide extent of the upper and lower aspects of the stem.

In the seizure and manipulation of the hairs the mandibles played a prominent role, aided by the guiding elements of the maxillae and the anterior pair of legs. When the hair was in place, the mandibles let go and the spinneret went into action.

At 12:15 A.M. whorl number five was finished, the last hair and silken cross-bar and the final guy rope in place. The larva again turned and faced up the blade. Then occurred an interpolation, what we human beings would call an afterthought. After taking a few steps upward, it hesitated, turned around, turned back to the just completed whorl, and put in an additional half dozen licks, paying out an inch or two of silk, and then without hesitation again headed up the narrow path. This action might have been instigated by an unused residue of instinct, some unfulfilled or unexpended ganglion urge. In any event, it was done before our eyes.

The larva now took up a position beneath and facing up the blade, coming to rest with its posterior hairs just touching the uppermost of the lower series of three whorls, and a body length from the single upper one. It rested quiet-

ly for twenty minutes. At 1.30 A.M. the larva made two abortive whorls at head and tail, and then rested.

The general aspect of the area was as follows:

3 lower whorls, 11 mm apart.
10 mm more to hinder end of larva.
20 mm length of slightly constricted larva.
4 mm to whorl in front of head.
16 mm to final upper whorl.
12 mm to tip of eaten stem, the distal 95 mm of blade length having been eaten during the day.
Total length of grass stem involved, 72 mm.

Including the two whorls at head and tail, the chronological sequence of the whorls was: lower 1, 2, 4, 5, (larva), 6, 3 upper. Thus the larva fenced itself in by a judicious sequence, from outer to inner. It may be significant that three well-formed whorls protected the possible approach of danger up the stem from the ground, while the unreachable, broken upper tip was guarded by a single complete whorl. The same principle is seen in the rat-guard of metal fastened midway down a cable from a vessel to the wharf.

At 1.47 A. M. the larva began a new series of contortions, differing in indescribable details from the pre-whorl activities. It swung first to one, then the other side, then began pulling out the short body hairs. These seemed less strongly fixed than the long ones. and by degrees the body became bare. These short hairs were arranged longitudinally upon an already spun, thin sheet of web encasing the grass blade and about half of the larva. They were fastened firmly with more of pure silk and fewer of the sticky drops. The contortions were now up and down, fore-and-aft, as necessitated by the boatlike casing of silk, a half cocoon, enveloping the lower half of the larval body.

The head and thoracic segments showed an even greater mobility than hitherto, and the mandibles reached up and "mouthed" the hairs of the dorso-median brushlike tuft. The spinneret moved around them near the base, binding a few at a time into a dense, close sheaf. Finally the mandibles were pushed into the crowded base, and a considerable number of hairs was pulled out. It took five or six trips, with the mandibles filled with sheaves of hairs, for the entire brush to be transplanted from the dorsal part of the segment to the sheet of silk lying on the cephalic cap. When replanted in an oblique position, and the larval head reinserted in the head cap of silk and short hairs, the tuft appeared as if springing directly up from the surface of the great rounded epicranial plates which formed the dominant, bulging area of the head proper.

A still more difficult feat was the cutting and conveying of the posterior brush, but in time, in what was darkness to the larva, and in the early morning hours, the feat was accomplished Most of the posterior tuft was fastened alongside of the grass blade itself, whence it curved up and extended obliquely outward.

This was only the first part of this operation. After the planting of the brush, the energetic caterpillar began on the remaining long hairs, those left after the completion of the whorls. Twenty to thirty of these hairs were now plucked bodily from the larva and bound around the brush, extending far beyond it in an elongated wisp. Then a similar operation was accomplished around the posterior brush. There seemed no end to the patient industry and the driving instinct of the small caterpillar.

The result was a decided similarity in the fore-and-aft appearance. The final aspect was of a short bit of debris, adhering to and inferiorly parallel with the grass blade, with an irregular protuberance projecting at each end. The whole was protected by the almost invisible but efficient whorls.

At 3 A.M. the whole complex operation seemed complete, and at 6 A.M. the larva had not moved. I had kept continuous watch, and whenever a new phase became apparent I summoned my associates to see it, to examine the details of action with a hand lens, to verify every part of this amazing performance.

March 11 found the larva still suspended from the head and tail caps, with the thin sheet of silk amidships. At 10 A.M. the pupation was almost complete, and the shed skin was being shunted into the tail cap. The chrysalid was brown, set off by the clear, pale orange of the outlines of the wings and abdominal segments. For some time the chrysalid remained suspended by head and tail caps, with an alarming amount of sagging medially. A quarter of an hour later, this slack had been taken up and the pupa was stretched tightly along the under side of the grass stem.

Ten days later, on March 21, the moth hatched, a clear-winged, black-bordered, red-tailed euchromid. It emerged from an anterior ventral crevice without displacing the cephalic cup and tuft, or disturbing any of the whorls. In ten minutes the wings appeared full-sized but thickened, with fluid still in them. The moth hung vertically, wings together, like many butterflies. Ten more minutes and the wings were slowly flattened, euchromidlike.

We have only two instances of the reactions of wandering insects to the succession of whorls. The first was another individual caterpillar of the same species, which found its way to a new blade supporting a chrysalid and series of whorls.

It began feeding at the tip of the stem, intent on its adventitious feeding and quite oblivious of the defences, but when it encountered the first whorl, it dangled half of its body in mid-air, continuing to feed. Then twisting the posterior end of the body and the last pair of prolegs, it climbed backward *around* the whorl. In an encounter with another whorl it devoured several of the long hairs which obstructed its path. It finally made its way to the base and then walked away from the stem, leaving the chrysalid and most of the whorls undisturbed.

One day, with difficulty, I persuaded several ants to climb about the grass blade below the lowermost whorl. All but one approached, antennaed the base of the whorl, turned and made their way to the base, and vanished. The effect was as if the whorls were defended by an unpleasant odor rather than by mechanical difficulties.

The remaining ant investigated more thoroughly. It climbed out a short distance along the radii, making two separate attempts, and then gave up. It was certainly not an out and out attempt to overcome the barrier, but even so, it failed to pass or reach the periphery of the whorl.

On following days, we watched the making of other whorls, and took still and motion pictures of the whole process.

EXPLANATION OF THE PLATES

Plate I

Fig. 1. Full-grown caterpillar of the euchromid moth, *Aethria carnicauda* Butler. No. 5330. × 2.4.

Fig. 2. Chrysalid of same caterpillar protected by whorls of hairs. Note disposition of tufts. × 2.

Plate II

Fig. 3. Adult female moth emerged from chrysalid in Fig. 2. × 2.

Fig. 4. First published illustration of hair whorls of a closely related species, *Dinia aeagrus* (Cramer).

Figs. 1, 2 and 3. Photographs by Rosemary Kenedy.
Fig. 4. After Fritz Müller.